Literature

Bader, R. S.; Hall, J. S. (1960): Osteometric variation and function in bats. Evolution **14**, 8—17.

Black, C. C. (1963): A review of the North American Tertiary Sciuridae. Bull. Mus. Comp. Zool. **130**, 109—248.

Harman, H. H. (1967): Modern factor analysis. 2nd ed. Chicago: Univ. Chicago Press.

Long, C. A.; Kamensky, P. (1967): Osteometric variation and function of the high-speed wing of the free-tailed bat. Amer. Midl. Nat. 77, 452—461.

Long, C. A.; Captain, J. (1974): Investigations on the sciurid manus. I. Some new taxonomic characters and their importance in the classification of squirrels. Z. Säugetierkunde **39**, 98—102.

Olson, E. C.; Miller, R. A. (1958): Morphological integration. Chicago: Univ. Chicago Press.

Piterka, H. E. (1936): A study of the myology and osteology of tree sciurids with regard to adaptation to arboreal, glissant and fossorial habits. Trans. Kansas Acad. Sci. 39, 313—332.

Savile, D. B. O. (1957): Adaptive evolution in the avian wing. Evolution **11**, 212—224.

Van Valen, L. (1965): The study of morphological integration. Evolution **19**, 347—349.

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Reproduction of the multimammate rat, *Praomys (Mastomys) natalensis* (Smith), in Uganda

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Introduction

Multimammate rats are common throughout Africa south of the Sahara. They usually live in savanna, cultivated land, or around human habitation. Their growth and breeding biology has been studied in many areas because they are important carriers of human plague and they may also be serious agricultural pests (Kingdon 1974).

The specific validity of the various described forms is open to question. Chromosome studies have revealed that the form *natalensis* (Smith) from South Africa has 36 chromosomes, the West African form *erythroleucus* (Temminck) has 38 chromosomes, and another unnamed form from West Africa has 32 chromosomes (Matthey 1966, 1973). The relationship of Uganda *Mastomys* to these species is not known. They are provisionally referred to the form *natalensis* (Delany 1975), but chromosome studies are required to help determine their status in relation to the South and West African forms.

Studies by Brambell and Davis (1941) in Sierra Leone, Chapman et al. (1959) in Tanzania, Dieterlen (1967) and Pirlot (1954) in Zaire, Sheppe (1972, 1973) in

Z. Säugetierkunde 42 (1977) 221—231

ISSN 0044—3468/ASTM-Coden ZSAEA 7

Zambia, HANNEY (1965) in Malawi, SMITHERS (1971) in Botswana, and COETZEE (1965) in South Africa have indicated that the breeding activity of multimammate rats is possibly related to the pattern of rainfall. However, the seasonal variation of photoperiod and, in some cases, temperature is similar to that of the rainfall in these areas. Therefore, it is not possible to determine with the information presently available which environmental cues are being used to regulate breeding activity.

This report describes the breeding biology, body growth, and population structure of *Mastomys* collected in the Ruwenzori (formerly Queen Elizabeth) National Park in Western Uganda. The study is significant because the study population was located in an area where the effects of photoperiod and temperature on breeding activity could be eliminated because they were virtually constant throughout the year. A brief report on the breeding pattern of this species compared with other rodent species living in the same area is provided by DELANY and NEAL (1969).

Study areas and climate

Most animals were collected from the Crater Track region (0° 06' S, 29° 54' E) within an area of approximately 8 km², 8–11 km south of the equator at an altitude of 1000–1100 m. There were few bushes or trees in the area, and the three major grass communities, dominated by *Imperata cylindrica*, *Cymbopogon afronardus*, and *Themeda triandra*, formed a dense cover 90–120 cm high. Part of the area was burnt in July 1965 and subsequent collections were made in both burnt and unburnt areas. NEAL (1970) provides a more detailed description of the area.

A few animals were also collected in the Royal Circuit area located approximately 1 km south of the Crater Track region at an altitude of 975 m. The vegetation was very similar to that of the Crater Track except for the absence of *Cymbopogon*.

The climate was monitored at Mweya Peninsula located approximately 12 km south of the main study area. Seasonal changes in photoperiod were negligible because the area was located so close to the equator. The mean monthly temperature varied 1 °C (range 22.9–23.9 °C) during the period of study. The maximum temperature recorded was 32.7 °C and the minimum 14.5 °C. Rainfall was seasonal. There are normally two rainy seasons, during the periods March until May and September until November (MCCALLUM and HANNA 1969), although the exact dates vary slightly from year to year.

Materials and methods

A total of 388 *Mastomys* were trapped in the Crater Track region during a 14 month period from April 1965 until May 1966. An additional 40 animals were trapped in the Royal Circuit area during late June 1965. The animals were measured, weighed, and sexed. The gut (from the lower oesophagus to the rectum) was removed and its weight was subtracted from the total weight to obtain a clean body weight. The weight of the uterus and embryos was also subtracted in the case of pregnant females. The carcass was then dissected to determine its reproductive condition.

The paired testes, vesiculae seminales, and epididymides were removed, and weighed after preservation in Bouin's solution. A sperm smear was taken from each cauda epididymis before fixation, and the relative abundance of sperm determined microscopically. The males were categorized as follows: 0 = no sperm present; ½ = only a few sperm visible amongst fat globules, or very few sperm present; 1 = sperm abundant. Only animals in the last class were considered to be fecund.

The female reproductive tract and mammae were examined before fixation. Females were classed as a. lactating, if milk could be expressed from the nipples or if the placental scars were very recent (see below); b. pregnant, if macroscopically visibly pregnant; c. parous, if placental scars were observed; d. mature, if corpora lutea were present and/or the uterus was well vascularized and swollen; e. immature, if the uterus was very thin and no corpora lutea were observed. Mature females were also classified as anoestrus if the uterus was thin and poorly vascularized; reproductively active, if the uterus was slightly swollen and well vasculated; or in oestrus, if the uterus was red and swollen. The number of live and resorbing embryos in each uterine horn of pregnant females were recorded, and where possible the placental scars of parous females were counted. The placental scars were classed as very recent if they were large and still distended the uterus.

The skulls of all animals were cleaned and the relative age of each individual was determined by the degree of tooth wear (Neal 1968).

Results

Breeding season

There were two well-defined periods of breeding activity a year which were correlated with the bimodal rainfall pattern (Fig. 1 B, E). Oestrous females were first collected approximately one month after the onset of the rains and pregnancies first

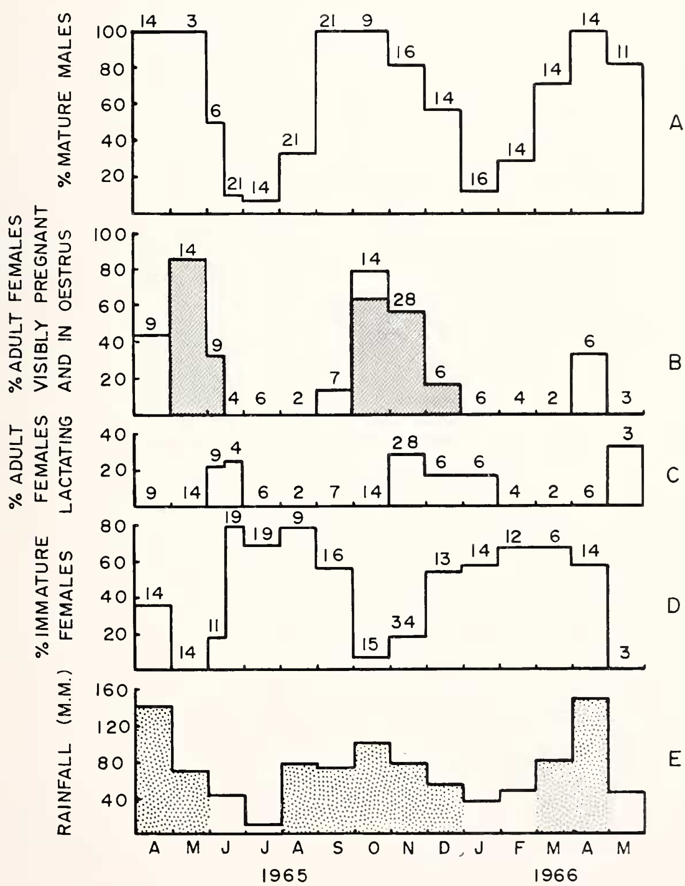

Fig. 1. Seasonal changes in reproductive activity of *Praomys (Mastomys) natalensis* in relation to monthly rainfall. The numbers over histograms A — D indicate sample sizes. In B, the cross hatched area represents pregnant females and the open area oestrous females. In E, the stippled area indicates the months when rainfall was greater than 50 mm

recorded two to four weeks later. Reproductive activity declined after an initial peak and ceased at the end of the rains or beginning of the dry season. Females were in a state of permanent anoestrus outside of the breeding periods. The occurrence of lactating and immature females (Fig. 1 C, D) was generally consistent with this pattern of breeding, but the absence of lactating females in July 1965 suggests that the litters of the June pregnancies failed to survive. Breeding activity was not significantly different in burnt and unburnt areas during the September–December breeding period.

The two breeding periods in 1965 were sufficiently long for some females to have two litters, because the gestation period is approximately 23 days (JOHNSTON and OLIFF 1954). Approximately one-fifth of the pregnant females collected in June and November were also lactating, which suggests that only a small proportion of the population successfully mated at the post-partum oestrus. Only one of 25 adult females collected immediately following the two breeding seasons was known to have had two litters.

The percentage of males that were mature was highly correlated with female breeding activity (Fig. 1 A), and there was a pronounced seasonal variation in the weights of the adult testes and vesiculae seminales (Table). The mean testes weight of adult males was 1.2 g during the April – June and September – December 1965 and April 1966 breeding periods, compared to a weight of 0.72 g for those collected during the July 1965 and January – February 1966 dry seasons. The difference in weight was highly significant ($t_{94} = 5.98 : P < 0.001$). The regression of the vesiculae seminales was even more pronounced and occurred approximately one month before the testes regressed (see Table), contrary to that found in the Transvaal (COETZEE 1965). A few adult males (age classes X–XIII) were collected with reduced fecundity ratings in July and August 1965, and January 1966 (Fig. 2). COETZEE (1965) and SHEPPE (1973) also found a few post breeding males during the dry season in the Transvaal and Zambia. BRAMBELL and DAVIS (1941) and CHAPMAN

Table

Mean weights (in grams) and standard errors of monthly samples of paired testes and vesiculae seminales (SV) of adults and juveniles

Month	No.	adult		Apr.—May cohort			Oct.—Nov. cohort		
		Testes	SV	No.	Testes	SV	No.	Testes	SV
Apr.	14	1.29 ± 0.06	0.49 ± 0.05						
May	3	1.09 ± 0.02	0.87 ± 0.30						
June	6	1.05 ± 0.18	0.16 ± 0.04	3	0.03 ± 0.003	*			
July	3	0.68 ± 0.17	0.06 ± 0.01	11	0.05 ± 0.02	*			
Aug.	4	0.96 ± 0.19	0.13 ± 0.08	16	0.36 ± 0.06	0.02			
Sept.	19	1.12 ± 0.04	0.24 ± 0.03		Transferred to Adults				
Oct.	9	1.24 ± 0.05	0.57 ± 0.07						
Nov.	14	1.31 ± 0.05	0.56 ± 0.04				3	0.09 ± 0.03	*
Dec.	9	1.20 ± 0.07	0.29 ± 0.02				6	0.17 ± 0.06	0.002
Jan.	3	0.67 ± 0.26	0.08 ± 0.02				14	0.21 ± 0.07	0.003
Feb.	3	0.81 ± 0.20	0.05 ± 0.003				11	0.15 ± 0.04	0.003
Mar.	2	1.33 ± 0.05	0.13 ± 0.02				12	0.63 ± 0.07	0.02
Apr.	14	1.16 ± 0.05	0.43 ± 0.07					Transferred to Adults	
May	9	1.10 ± 0.08	0.10 ± 0.02	2	0.03 ± 0	*			

* Too small to measure.

et al. (1959) believed that males remained permanently in breeding condition after puberty in Sierra Leone and Tanzania, but their sample size was too small to be certain on this point.

The testes and vesiculae seminales of immature animals did not increase in weight during the dry seasons (Table). They increased rapidly in weight with increased rainfall, and all males were classed as fecund a month after the start of the rains. Hanney (1965) has also suggested that the sexual development of young males is delayed during the dry season in Malawi.

Body weights

The birth weight was estimated to be approximately 1.8 g from the weights of late-term embryos, compared to a mean weight of 2.2 g (range 1.9–3.0 g) for a laboratory population in the Transvaal (Meester 1960).

The smallest animals trapped weighed 10–15 g which is assumed to be the weight at the time of weaning. Other records of weanling weights are 11.7 g (Meester 1960) and 13 g (Johnston and Oliff 1954) for laboratory populations, and 10–20 g (Dieterlen 1967) and 20–25 g (Brambell and Davis 1941) for wild populations in Zaire and Sierra Leone.

The growth in weight of immature animals could be followed quite accurately because the recruitment of young was confined to short periods. Their growth during the periods June — September 1967 and November 1965 — March 1966 was approximately linear. Linear regression analysis revealed that males grew significantly faster than females, and the growth of both sexes during June — September was significantly faster than during the November — March period.

Both sexes weighted approximately 35 g at puberty which is less than the recorded weights of 39–45 g reported by Brambell and Davis (1941), Chapman et al. (1959), Davis (1963), Dieterlen (1967), Oliff (1953), and Pirlot (1957). There was a seasonal fluctuation of adult body weights which was most pronounced for the females. The weights increased during the rains and decreased by approximately 25 per cent during the dry seasons. The weight change is probably related to the seasonal cycle in body fat content (Field 1975). A similar seasonal fluctuation of adult body weight has been recorded in Zambia (Sheppe 1973).

Litter size

The mean number of implanted (i. e. live and resorbing) and live embryos of 41 pregnancies were 12.6 ± 0.21 (range 7–19) and 12.1 ± 0.26 (range 6–19) respectively. Other records of the mean number of embryos in *Praomys natalensis* are 9.8 (Dieterlen 1967) and 4.6 (Rahm 1970) in eastern Zaire, 13.4 in northern Tanzania (Reichstein 1967) and 11.2 (Chapman et al. 1959) in southern Tanzania, 11.0 in Malawi (Hanney 1965), 11.0 ± 0.46 in Zambia (Sheppe 1973), 10.0 in Botswana (Smithers 1971), and 9.5 in South Africa (Coetzee 1965). The mean number of embryos in *Praomys erythroleucus* in Sierra Leone was 11.8 (Brambell and Davis 1941). Thus, litter size appears to be similar in both species, with a suggestion that it might be highest near the equator and reduced at higher latitudes. The exceptionally small litter size reported by Rahm (1970) may reflect a habitat difference because the population was living in forest which is not its usual habitat. Sheppe (1973) has also reported local variations in litter size in Zambia which may reflect habitat differences.

It is difficult to make detailed comparisons between different areas because of seasonal variation and the relationship of litter size to maternal characteristics. In this study the variation in litter size in relation to the clean body weight of the mother and the month collected was analyzed by two-way analysis of variance. There was a significant ($P < 0.05$) decline in litter size as the breeding season progressed, but the consistently small increase in litter size with increased maternal weight was not statistically significant ($P > 0.25$). Coetzee (1965) and Sheppe (1973) also report a marked seasonal variation in litter size, which was at a maximum towards the end, rather than at the beginning, of the breeding season. The number of ova ovulated and the number of embryos have been reported to be positively correlated with the maternal body weight (Brambell and Davis 1941; Hanney 1965), and Oliff (1953) has shown a relationship between litter size and maternal age in a laboratory population.

Age structure

The monthly changes in age structure of the Crater Track population (Fig. 2) were consisistent with the pattern of breeding already described. The failure to catch animals in age class I in July 1965 and January 1966 suggests that individuals born at the end of both breeding seasons in 1965 were not succesfully weaned. The

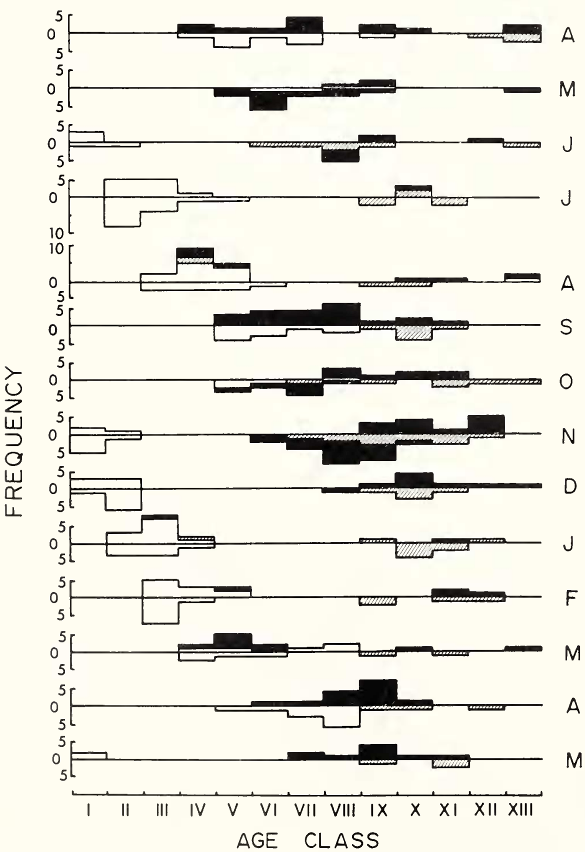

Fig. 2. Monthly age structure of *Praomys (Mastomys) natalensis.* Males are above each line and females below. Open blocks represent males with sperm rating 0 or nonparous and non-pregnant females; cross hatched blocks represents males with sperm rating 1/2 or parous nonpregnant females; and solid blocks represent males with sperm rating 1 or pregnant females

greatest mortality of young probably occurred before or soon after weaning because the breeding data indicated that the population should increase 7—8 times after each breeding season even if all the adults died, but the catch per unit effort only indicated about a twofold increase. The young did not start to reproduce until the breeding period following that of their birth. The males started to mature two months after being weaned, and most had matured three to four months after weaning. The females reached puberty approximately one month after the males. The main periods of adult mortality were soon after the breeding seasons when the population was largely replaced by juveniles. Similar observations have been made by Coetzee (1965) in the Transvaal and Sheppe (1973) in Zambia.

Discussion and conclusions

Breeding season

The location of this study was such that the effects of photoperiod and temperature on reproductive activity could be eliminated because they were virtually constant throughout the year. The lengths of the breeding seasons were directly related to the duration of the rains. This relationship is most clearly demonstrated by comparing the breeding activity in the two years of study during April, May, and June. Breeding continued until mid-June in 1965, but had ceased by mid-May 1966 apparently in response to the early onset of the dry season. A similar reduction in the length of the breeding season was also noted for *Lemniscomys striatus* and *Mus triton* (Delany and Neal 1969). Field (1975) studied the same Crater Track population in a year when the rains were advanced by one or two months. The rains began in January or February and although some breeding activity was inferred in February and March, presumably by some of the few remaining adults in the population, the main breeding period began at the usual time in April. Thus, there would appear to be certain constraints on the flexibility of the breeding response to changes in rainfall patterns. If the rains continue longer than usual it is probably that the breeding season would be similarly extended, but if the rains begin earlier than usual the breeding season may not be advanced as anticipated because the majority of the population consists of juveniles which may be unable to accelerate their prepubertal development.

The patterns of reproductive activity reported by the more detailed studies on multimammate rats are summarized in Fig. 3. In addition, pregnant *Praomys (Mastomys) erythroleucus* were collected in October, November, and December in Cameroun (Sanderson 1940) where the rainfall pattern is similar to that shown for Sierra Leone (Fig. 3); the breeding and rainfall patterns in Botswana (Smithers 1971) were similar to those shown for Zambia (Fig. 3); and breeding appeared to be confined to the end of the rains and beginning of the dry season in Meru National Park, Kenya (Neal, unpublished data). These studies indicate that the relationship of breeding activity to rainfall is variable. For example, the breeding season began before the onset of the rains in Zambia (Sheppe 1972, 1973), but only began well after the onset of rains in Malawi (Hanney 1965) and Uganda. These differences suggest that breeding activity is influenced by a complex of environmental factors rather than simply the direct and/or indirect effects af rainfall.

The environmental factors responsible for the initiation of breeding in multimammate rats remain to be elucidated. It appears most likely that their reproductive rhythm is regulated by a complex of environmental factors which vary according

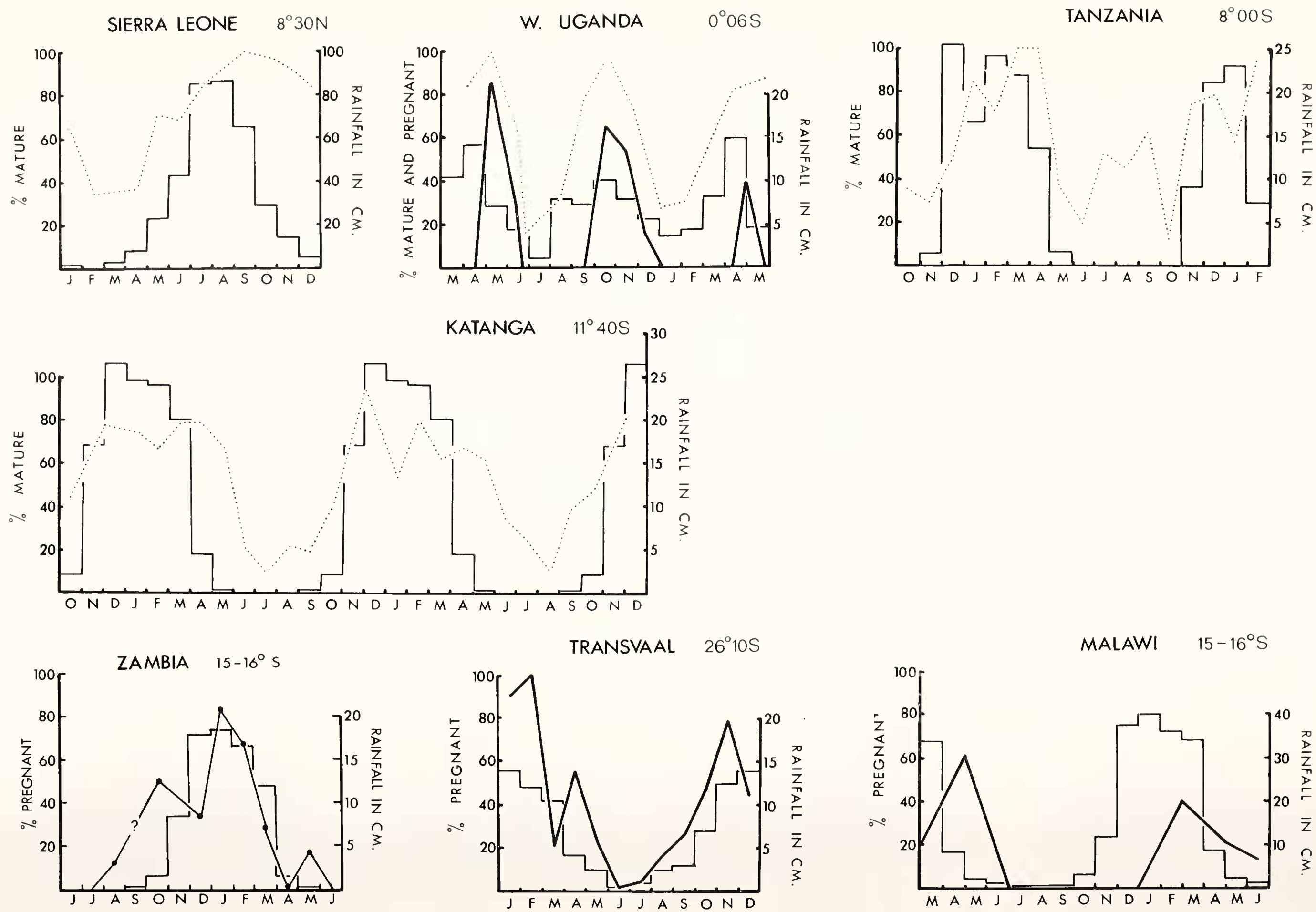

Fig. 3. Breeding activity of multimammate rats in Africa. Percentages of adult females are represented by stippled lines, and percentages of adult females that are pregnant are represented by solid lines. Mean monthly rainfall is represented by histograms. Rainfall data for Sierra Leone, Katanga, Malawi, Zambia, and Transvaal from Jackson (1961). Source of breeding data for Sierra Leone (Brambell and Davis 1941), W. Uganda (this study), Tanzania (Chapman et al. 1959), Katanga (Pirlot 1954), Zambia (Sheppe 1972), Malawi (Hanney, 1965), and Transvaal (Coetzee 1965).

to the locality, as suggested by MILLAR and GLOVER (1973) for the African rock hyrax. The direct and indirect (i. e. nutritional factors) effects of rainfall are the most likely proximate cause of the breeding season in the location of the present study. At other locations near the equator the pattern of reproduction might also be influenced by temperature. However, at higher latitudes the primary proximate cause may well be photoperiod with rainfall and temperature exerting a modifying influence.

The timing of the breeding season during the rains and early dry season is adaptive in at least three ways. Most of the young are born when food is abundant and nutritious (FIELD 1975) and when problems of water stress are slight, and breeding is at a minimum when the probability of savanna fires is greatest.

Demographic pattern

Mastomys has a particularly large litter size even for a murid rodent (DELANY 1972), and appears to have a short life expectancy. The mean life expectancy of the western Uganda population is particularly short because there is an almost complete turnover of the population twice yearly, whereas in most areas of Africa this turnover occurs annually. The high reproductive potential and low life expectancy is characteristic of an r-selected species and is a typical demographic pattern for a murid rodent (FRENCH et al. 1975). This strategy of population success has implication for the artificial control of this pest species. "For those dependent upon rapid rate of increase, control effort should be applied in a manner to effect productivity of the population, such as eliminating nest sites, modification of the sex ratio, or reducing fertility of the species. Effort devoted to altering the survival rate of the species, such as trapping or poisoning, would be expected to be less fruitful." (FRENCH et al. 1975).

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Summary

A total of 428 *Praomys (Mastomys) natalensis* were collected over a 14 month period in the Ruwenzori National Park, Uganda, to study the breeding biology and demographic pattern of the population.

There were two breeding seasons each year which appeared to be related to the bimodal pattern of rainfall.

During the dry seasons the females were in anoestrus, and there was a regression of the testes and vesiculae seminales of adult males.

Immature males grew faster and matured at an earlier date than females, and the body growth of immature animals was different during the two dry seasons.

The mean number of embryos was 12.6, and the litter size declined throughout the breeding season.

Age structure studies indicated that young born at the end of the breeding periods were not successfully weaned, and the main periods of adult mortality were immediately following the breeding seasons when the population was largely replaced by juveniles.

Zusammenfassung

Fortpflanzung der multimammaten Ratte, Praomys (Mastomys) natalensis (Smith) in Uganda

Insgesamt 428 *Praomys (Mastomys) natalensis* wurden 14 Monate lang im Ruwenzori National Park, Uganda, gesammelt, um die Fortpflanzungsbiologie und die demographischen Verhältnisse des Rattenbestandes zu studieren.

Es ließen sich zwei Fortpflanzungsperioden pro Jahr feststellen, die in Bezug zum bimodalen Charakter des Niederschlags zu stehen schienen.

Während der Trockenperiode waren die Weibchen unfruchtbar, und es zeigte sich eine Zurückbildung der Hoden und Vesiculae seminalis bei ausgewachsenen Männchen.

Noch nicht voll entwickelte Männchen wuchsen schneller und entwickelten sich zu einem früheren Zeitpunkt als die Weibchen, und das Körperwachstum der unentwickelten Tiere verhielt sich unterschiedlich während der zwei Trockenperioden.

Die Durchschnittsanzahl der Embryonen belief sich auf 12.6, und die Wurfstärke ging während der Fortpflanzungsperiode zurück.

Altersstrukturstudien zeigen, daß Neugeborene am Ende der Fortpflanzungsperiode nicht erfolgreich entwöhnt waren, und die Periode mit der höchsten Sterblichkeitsrate der Erwachsenen sogleich nach den Fortpflanzungsperioden folgte, wenn der Rattenbestand weitgehend durch junge Ratten aufgefüllt wurde.

References

Brambell, F. W. R.; Davis, D. H. S. (1941): Reproduction of the multimammate mouse *(Mastomys erythroleucus* Temm.) of Sierra Leone. Proc. zool. Soc. Lond. **111** B, 1—11.

Chapman, B. M.; Chapman, R. F.; Robertson, I. A. D. (1959): The growth and breeding of the multimammate rat *Rattus (Mastomys) natalensis* (Smith) in Tanganyika Territory. Proc. zool. Soc. Lond. **133**, 1—9.

Coetzee, C. G. (1965): The breeding season of the multimammate mouse *Praomys (Mastomys) natalensis* (A. Smith) in the transvaal Highveld. Zool. Afr. **1**, 29—39.

Davis, D. H. S. (1963): Wild rodents as laboratory animals and their contribution to medical research in South Africa. S. Afr. J. med. Sci. **28**, 53—69.

Delany, M. J. (1972): The ecology of small rodents in tropical Africa. Mammal Review **2**, 1—42.

— (1975): The rodents of Uganda. London: Brit. Mus. Natural Hist.

— Neal, B. R. (1969): Breeding seasons in rodents in Uganda. J. Soc. Reprod. Fert. (Suppl.) **6**, 229—236.

Dieterlen, F. (1967): Jahreszeiten und Fortpflanzungsperioden bei den Muriden des Kivusee-Gebietes (Congo). Z. Säugetierkunde **32**, 1—44.

Field, A. C. (1975): Seasonal changes in reproduction, diet and body composition of two equatorial rodents. E. Afr. Wildl. J. **13**, 221—235.

French, N. R.; Stoddart, D. M.; Bobek, B. (1975): Patterns of demography in small mammal populations. In: Golley, F. B.; Petrusewicz, K.; Ryszkowski, L. (Eds.), Small mammals: their productivity and population dynamics. Cambridge University Press: Cambridge.

Hanney, P. (1965): The Muridae of Malawi (Africa: Nyasaland). J. Zool., Lond. **146**, 577—633.

Jackson, S. P. (1961): Climatological Atlas of Africa. Pretoria: Government Printer.

Johnston, H. L.; Oliff, W. D. (1954): The oestrous cycle of female *Rattus (Mastomys) natalensis* (Smith) as observed in the laboratory. Proc. zool. Soc. Lond. **124**, 605—613.

Kingdon, J. (1974): East African Mammals. An Atlas of Evolution in Africa. Vol. II, part B. Hares and Rodents. London: Academic Press.

McCallum, D.; Hanna, L. W. (1969): Climate. In: Atlas of Uganda. Entebbe: Dept. of Lands and Surveys.

Matthey, R. (1966): Cytogenetique et taxonomie des rats appartenant au sous-genre *Mastomys* Thomas (Rodentia-Muridae). Mammalia **30**, 105—119.

— (1973): The chromosome formulae of Eutherian Mammals. In: Chiarelli A. B.; Capanna, E. (Eds.), Cytotaxonomy and Vertebrate Evolution. London: Academic Press.

Meester, J. (1960): Early post-natal development of multi-mammate mice *Rattus (Mastomys) natalensis* (A. Smith). Ann. Transv. Mus. **24**, 35—52.

Millar, R. P.; Glover, T. D. (1973): Regulation of seasonal sexual activity in an ascrotal mammal, the rock hyrax, *Procavia capensis*. J. Soc. Reprod. Fert. (Suppl.) **19**, 203—220.

Neal, B. R. (1968): The ecology of small rodents in the grassland community of the Queen Elizabeth National Park, Uganda. Ph. D. thesis, Univ. Southampton.

Neal, B. R. (1970): The habitat distribution and activity of a rodent population in Western Uganda, with particular reference to the effects of burning. Revue Zool. Bot. afr. **81**, 29—50.
Oliff, W. D. (1953): The mortality, fecundity and intrinsic rate of natural increase of the multimammate mouse *Rattus (Mastomys) natalensis* (Smith) in the laboratory. J. Anim. Ecol. **22**, 217—226.
Pirlot, P. L. (1954): Pourcentages de jeunes et périodes de reproduction chez quelques Rongeurs de Congo belge. Annls. Mus. r. Congo belge Sér. 4to Zoologie **1**, 41—46.
— (1957): Croissance et maturité sexuelle chez *Mastomys coucha* Smith. Mammalia **21**, 385—395.
Rahm, U. (1970): Note sur la reproduction des Sciuridés et Muridés dans la forêt équatoriale au Congo. Revue suisse Zool. 77, 635—646.
Reichstein, H. (1967): Populationsstudien an steppenbewohnenden Nagetieren Ostafrikas. Z. Säugetierkunde **32**, 309—313.
Sanderson, I. T. (1940): The mammals of the North Cameroons Forest Area being the results of the Percy Sladen Expedition to the Mamfe Division of the British Cameroons. Trans. zool. Soc. Lond. **24**, 623—725.
Sheppe, W. A. C. (1972): The annual cycle of small mammals populations on a Zambian flood plain. J. Mammal. **53**, 445—460.
— (1973): Note on Zambia Rodents and Shrews. The Puku **7**, 167—190.
Smithers, R. H. N. (1971): The mammals of Botswana. Salisbury: Nat. Mus. Rhodesia.

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Rhythmic pigmentation in Porcupine quills

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Introduction

Porcupines show a striking alternation between black and white regions down the length of their quills. Such quills, which represent modified hairs, are far easier to examine than similarly banded hair from other mammalian sources, and they invite a study of pigment patterning which could be relevant for pigment function generally.

The purpose of this investigation was to establish the main features in the pattern of quill pigmentation, and hence the steps required in generating patterns of this type. Sets of loose quills from 3 porcupines and quill-covered skins from 5 other specimens were available, all belonging to *Hystrix africaeaustralis*.

Z. Säugetierkunde 42 (1977) 231—239

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